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3 LONGITUDINAL ANALYSIS OF *PLANTAGO*: ADAPTIVE BENEFITS OF ITEROPARITY

4 IN A SHORT-LIVED, HERBACEOUS PERENNIAL

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16 ABSTRACT. Theory suggests that iteroparity may confer greater fitness than semelparity in
17 situations in which temporal environmental variation is high and unpredictable. Variable
18 age-specific mortality, density dependence, and other factors may also favor iteroparity over
19 semelparity. Here, we empirically test the adaptive benefits of greater numbers of reproductive
20 years in a study of reproductive schedules in an experimental population of a short-lived
21 polycarpic perennial, *Plantago lanceolata*. A large experimental population was established that
22 included four cohorts with similar genetic structure. Individuals were censused for mortality,
23 size, and reproduction for seven years. Plants experienced variable numbers of reproductive
24 years, but one or two years were most common (~46.7% of the population reproduced only
25 once). The probability of flowering at least once prior to death was determined strongly by
26 extrinsic, environmental or intrinsic but environmentally-influenced variables, including
27 early-life size, cohort, and block, but also varied with a number of interactions involving
28 paternal lineage. Maternal effects explained small but significant components of the variance in
29 the number of reproductive years among individuals in each cohort, while paternal effects were
30 significant in only two cohorts. Number of reproductive years contributed significantly to
31 fitness in this system, more so than all other variables tested, although most of the variation in
32 relative fitness may be attributed to ultimately environmental influences. We suggest that the
33 high proportion of each cohort composed of plants reproducing only once may be due to

34 environmental constraints on either growth or size. Such environmental influences, particularly
35 on early life size, may result in small but important indirect effects on fitness.

36 *Key words:* inflorescence; iteroparity; reproductive schedule; reproductive timing; semelparity.

37 INTRODUCTION

38 Reproductive schedules cause and are a result of complex interactions of life history
39 relationships, population dynamics, and environment. Work on this topic was originally spurred
40 by Laurent Cole's proposition that the perennial growth habit, in which organisms live and
41 reproduce for more than one year, represents little fitness advantage over the annual habit (Cole
42 1954). Cole's hypothesis is at odds with the commonness of biennial and perennial plants
43 (Silvertown 1983, 1986), and rests on the assumptions of no age-specific mortality and no
44 density-dependence. Models breaking these assumptions suggest that delayed reproduction and
45 iteroparity may indeed be favored under some conditions (Charnov and Schaffer 1973, Bulmer
46 1985). Others have suggested that iteroparous perenniality may be favored under a range of
47 other conditions, including factors such as the duration of the reproductive season (Iwasa and
48 Cohen 1989), size at maturity (Baskin and Baskin 1979), the duration of the juvenile stage
49 (Stearns 1992), correlations among life history traits (Orzack and Tuljapurkar 1989), stochastic
50 environmental variability (Harper and White 1974, Orzack and Tuljapurkar 1989), and the
51 extent and timing of temporal variability in survival with respect to age (Bulmer 1985). Longer

52 lifespans in general also appear to be more common under a range of ecological conditions,
53 including even the type of community that organism typically lives in (Ehrlén and Lehtilä
54 2002).

55 Though theoretical work on the significance of different reproductive schedules is
56 substantial, empirical studies have focused mostly on obligately semelparous organisms,
57 including monocarpic plants. Fitness in monocarpic perennials has been found to be a function
58 of growth, probability of flowering, probability of survival, and reproductive output (c.f.
59 Metcalf et al. 2003). Here, size acts as an important determinant in the optimal flowering
60 strategy because of its importance in determining the probabilities of flowering and survival
61 (Harper and White 1974, Lacey 1986, Wesselingh and de Jong 1995). The optimal reproductive
62 schedule in a monocarpic perennial can be thought of as the schedule that optimizes
63 reproduction in the face of environmental variation and increasing mortality risk with age, and
64 is mediated by size and the marginal impact of growth (Lacey et al. 1983, Metcalf et al. 2003).

65 The evolutionary ecology of reproductive schedules is much less understood in iteroparous
66 organisms than in semelparous organisms. In polycarpic perennials, plants that reproduce
67 multiple times during their lifetime, reproduction may be delayed for many years, and the
68 probability of flowering often correlates positively with size and either positively or negatively
69 with future survival (Law 1979, Bierzychudek 1982, Shefferson 2006). Because polycarpic

70 perennials may flower any number of years within their lifespan, the number of reproductive
71 years may be subject to selection. In turn, the optimal age of reproduction may vary with the
72 number of reproductive events, because these plants do not need to “put all of their eggs in one
73 basket” as a monocarpic plant would. In iteroparous animals, years of reproduction may also
74 vary with conditions experienced in early life, because of the effects of such conditions on the
75 age of first reproduction, the onset of ageing, and fitness (Metcalfe and Monaghan 2001,
76 Nussey et al. 2007). Reproductive timing in polycarpic perennials should be adaptively plastic
77 in response to temporal and spatial variability in the environment. At the extreme end of
78 temporal variability, multiple reproductive events may result in a “spreading of risk” similar to
79 a bet-hedging trait (Slatkin 1974, Gillespie 1977), in which the effort put into reproduction in
80 any given year is lower than possible in order to increase the number of later reproductive
81 opportunities.

82 Here, we assess adaptive effects of iteroparity by assessing the fitness consequences of
83 different numbers of reproductive years in an experimental population of the short-lived,
84 polycarpic perennial *Plantago lanceolata*. In our experimental population, four cohorts with
85 similar genetic structures were planted in the same environment. Because they were planted in
86 different years, they had different environmental histories through their life cycles. We
87 hypothesize that these different environmental histories should result in different reproductive

88 schedules across cohorts, and have different fitness consequences even though each cohort has
89 a similar genetic background.

90 METHODS

91 *Field methods*

92 *Plantago lanceolata* L. is a short-lived, polycarpic perennial monocot with a widespread,
93 holarctic distribution. It is commonly found in disturbed habitats. The plant produces a basal
94 rosette from which it grows one or more long inflorescences. In central Virginia, flowering may
95 occur from April to September, though May to August is most common.

96 We obtained *Plantago* individuals from a wild population in Shadwell, Virginia. We then
97 bred five unique sets of sires and dams in the greenhouse according to a modified North
98 Carolina II breeding design (Comstock and Robinson 1948, 1952, Lynch and Walsh 1998), in
99 which each set was composed of four sires bred fully factorially with each of two dams. This
100 design resulted in a total of 40 parental combinations with approximately 800 seeds each. Seeds
101 from each resulting lineage were split into four cohorts, which were sequentially planted in the
102 greenhouse and grown until seedlings. The protocol established in an earlier study (see Roach
103 2003) for raising seedlings, planting, and marking individuals was also used for this study.
104 Seedlings of uniform age (approximately six weeks) were planted in a randomized block design
105 with replication of genotypes and cohorts. Plants were located 15 cm apart in rows each 20 cm

106 apart within an approximately $75 \times 45 \text{ m}^2$ area. This spacing was sufficient to avoid
107 competition between individuals and is within the natural density of the field. The analysis
108 presented here is for a subset of 21,406 plants from a larger experimental population (“large
109 families” only, see Roach et al. (*In press*)). The different cohorts were planted as follows:
110 October 2000, cohort 1, 6654 plants; October 2001, cohort 2, 7892 plants; October 2002, cohort
111 4, 3258 plants; and in the spring, April 2002, cohort 3, 3602 plants. This study includes data
112 from the time of planting until December 2007, by which time approximately 92% of the
113 experimental plants had died. Mortality was censused monthly. Additionally, we measured size,
114 as the total number of leaves per plant, in May and November of each year. Leaf number is
115 highly correlated with aboveground biomass ($r=0.70$, $P<0.0001$, $n=80$; D. Roach unpublished).
116 Mature inflorescences were counted and collected per plant throughout the flowering season.

117 *Analytical methods*

118 We first assessed basic patterns in reproductive schedule across cohorts. We began by
119 calculating the number of reproductive years that *Plantago* individuals experienced. We also
120 sought to explore the variation in age of first reproduction by assessing year of reproduction in
121 plants that reproduced only once prior to death. A year of reproduction was defined as any year
122 in which at least one inflorescence was produced. We then tested for genetic and environmental
123 impacts on probability of flowering at least once prior to death via logistic regression in SPSS

124 16.0 for Windows (SPSS Inc., Chicago, Illinois, USA), in which the probability of flowering
125 was dependent on size toward the start of the first growing season (hereafter referred to as
126 early-life size), lifespan (given in weeks), paternal lineage, and block were the independent
127 factors. This analysis was conducted separately for each cohort. In cohort 3, we skipped
128 flowering in the first growing season and instead began with the second growing season,
129 because these plants were planted after their first growing season had already begun. Also, all
130 plants surviving through the end of the study were set at a lifespan equivalent to having died in
131 December 2007, in order to simplify analyses (total plants still alive in Dec 2007 by cohort:
132 cohort 1, 353; cohort 2, 711; cohort 3, 500; cohort 4, 551).

133 We next asked if there was evidence of heritable genetic variation in number of
134 reproductive years. We assessed genetic components of variance in the number of reproductive
135 years among plants using variance components estimation via the VARCOMP procedure in
136 SPSS 16.0 for Windows (SPSS Inc., Chicago, Illinois, USA). Here, the number of reproductive
137 years was modeled as a function of dam, sire, and dam \times sire interaction as random factors in
138 an ANOVA-style analysis with type 1 sum of squares estimation and no intercept. The number
139 of reproductive years was standardized to a mean of 0 and a standard deviation of 1. Significant
140 genetic variation was inferred if both paternal and maternal components of variance were
141 significant, while maternal effects were inferred if maternal components were significantly

142 greater than paternal components.

143 We explored the factors determining fitness via path analysis (Scheiner 2000, Scheiner et al.
144 2002) using the AMOS package for SPSS 16.0 for Windows (SPSS Inc., Chicago, Illinois,
145 USA). The model determining relative fitness included early-life size, age of first reproduction
146 (in years), total reproduction in the first growing season, lifespan (in weeks), and the number of
147 years of reproduction (Figure 1). Total reproduction in the first year is the number of
148 inflorescences produced in that year (Roach 2003). Relative fitness is the total number of
149 inflorescences produced throughout life, standardized within each cohort to a range of 0 to 1
150 (i.e., 0 inflorescences = 0 fitness, and the fitness of the plant with the most inflorescences
151 produced = 1). All variables other than relative fitness were standardized to a mean of 0 and a
152 standard deviation of 1.

153 RESULTS

154 Cohorts varied in size and reproductive schedule. Plants in cohort 1 grew to the largest size
155 in their first year, while plants in cohort 4 grew to the smallest (size in Nov following first
156 growing season: cohort 1: 15.40 ± 0.185 leaves, cohort 2: 11.16 ± 0.170 leaves, cohort 3: $8.23 \pm$
157 0.195 leaves, cohort 4: 8.92 ± 0.260 leaves). Plants in cohort 1 were most likely to reproduce
158 twice while plants in all other cohorts were most likely to reproduce only once prior to death
159 (Figure 2). Plants that only reproduced once in their lifetimes did so primarily in the first or

160 second year, with plants in cohort 1 reproducing evenly among those ages, plants in cohort 2
161 reproducing mostly at age 2, and plants in cohorts 3 and 4 reproducing mostly in their first year
162 (Figure 3). Plants that reproduced only once prior to death lived approximately one extra year
163 after flowering (cohort 1: 1.2 ± 0.2 yrs, cohort 2: 1.2 ± 0.1 yrs, cohort 3: 1.4 ± 0.1 yrs, cohort 4:
164 1.4 ± 0.1 yrs, mean ± 1 SE).

165 The probability of flowering was strongly determined by size and lifespan in our study, with
166 cohort and block also significant (Table 1). Sire was not a significant main effect. However,
167 significant cohort \times sire, sire \times size, and sire \times lifespan interactions suggest that the probability
168 of flowering does have some genetic variation, and in particular that plant genotypes respond
169 plastically to different environments (Table 1). Significant cohort \times size and block \times size
170 interactions likewise suggest that the influence of size on reproductive schedules differs with
171 environments (Table 1).

172 The variance in the number of reproductive years among plants was strongly
173 environmentally determined, though not entirely so. Small, intrinsic components of variance
174 explained significant portions of the total variance in all cohorts (Table 2). Of these, maternal
175 effects were significant and strong relative to paternal effects in all cohorts (cohort 1: $F_{10,15} =$
176 3.257 , $P = 0.019$; cohort 2: $F_{10,15} = 3.799$, $P = 0.010$; cohort 3: $F_{10,15} = 3.930$, $P = 0.009$; cohort
177 4: $F_{4,20} = 5.313$, $P = 0.004$) (Table 2). Paternal components were significant only in cohorts 2

178 and 3, suggesting minor levels of heritable, additive genetic variance (Table 2).

179 Path analysis suggested that number of reproductive years significantly determined relative
180 fitness via direct paths in all cohorts, and did so more than any other tested factor in all cohorts
181 (Fig. 1, Electronic Appendix S1). Early-life size had a significantly negative influence on the
182 age of first reproduction, and a significantly positive influence on the amount of reproduction in
183 the first year (Fig. 1, Electronic Appendix S1). Further, greater reproduction in the first year of
184 life led to longer lifespan and greater relative fitness (Fig. 1, Electronic Appendix S1),
185 suggesting no cost of reproduction. Earlier age of first reproduction led to greater number of
186 reproductive years, as did longer lifespan (Fig. 1, Electronic Appendix S1). Greater
187 reproduction in the first year of life led to greater overall fitness, as did increased number of
188 reproductive years (Fig. 1, Electronic Appendix S1).

189 A number of effects varied among cohorts, suggesting the importance of environmental
190 variation both on development and fitness. Early-life size had a significantly negative effect on
191 lifespan in cohort 1, but a significantly positive effect in cohort 2, and no significant effects in
192 cohorts 3 and 4 (Fig. 1, Electronic Appendix S1). Age of first reproduction had a significantly
193 positive effect on lifespan in cohorts 2, 3, and 4, but not in cohort 1 (Fig. 1, Electronic
194 Appendix S1). Early-life size in the first year had a significantly positive effect on relative
195 fitness in cohorts 1, 2, and 3, but not in cohort 4 (Fig. 1, Electronic Appendix S1). Age at first

196 reproduction had a small but significantly negative effect on relative fitness in cohort 1, but no
197 effect in the other cohorts (Fig. 1, Electronic Appendix S1). Lifespan had a small but
198 significantly negative effect on relative fitness in cohorts 1 and 2, but no significant effect in
199 cohorts 3 and 4 (Fig. 1, Electronic Appendix S1).

200 DISCUSSION

201 Temporally-variable environments can produce dramatic differences in optimal
202 reproductive timing in monocarpic perennials (Lacey et al. 1983, Rees et al. 1999, Rees et al.
203 2004). We suggest that this may happen in short-lived polycarpic perennials such as *Plantago*
204 *lanceolata* because we found genetic variation, relationships between life history traits varying
205 across cohorts, and differential reproductive scheduling across years and cohorts (Tables 1 and
206 2, Electronic Appendix S1). In the monocarpic triennial *Daucus carota*, variation in the year of
207 reproduction was determined by both genetic and habitat variation (Lacey 1986). In a recent
208 study of an experimental population of the monocarpic evening primrose, *Oenothera biennis*,
209 genetic variation in annual vs. biennial reproductive strategy was found (Johnson 2007).

210 *Plantago* individuals may benefit from iteroparity by fine-tuning their reproductive
211 response to their environment. Reproductive traits in *Plantago* may often be plastic because of
212 the influence of temporal variability in such traits on several key components of fitness (Lacey
213 and Herr 2005). Further, a variety of environmental influences can cause variation in

214 reproductive timing even within a growing season, including the heights of surrounding
215 vegetation and the timing of disturbance events (van Tienderen and van der Toorn 1991a, b,
216 Hautekèete et al. 2002). Such plasticity in reproductive schedules, and in life histories in
217 general, is supported by the dramatic differences among cohorts. Cohort 1 in particular showed
218 greater lifespan and fitness with earlier age of reproduction, but the opposite patterns occurred
219 in the other cohorts (Table 3). Such patterns may be the result of plants in cohort 1 growing to
220 nearly twice the size of plants in other cohorts while in their first year. Further, plants that
221 reproduced only once had a post-reproductive life that averaged more than one year and thus
222 they could have reproduced another time. Among-cohort differences in the timing of
223 reproduction among plants, particularly among paternal lineages, reinforce that perenniality
224 may allow the plant to deal with year-to-year environmental stochasticity (Metcalf et al. 2003).
225 Such plasticity may be an important determinant of *Plantago*'s distribution, due to the
226 advantages it confers in the colonization of novel habitats (Williams et al. 1995, Maron et al.
227 2004).

228 The optimal reproductive schedule in *Plantago lanceolata* is likely to be influenced strongly
229 by early-life environment. The design of this experimental population, with individuals from
230 different cohorts having the same genetic structure and sharing the same environment, showed
231 cohort variation in a number of key reproductive traits. The environment is likely to influence

232 *Plantago*'s fitness via immediate impacts on growth during these early months. This may be
233 partially due to greater mortality in early ages, a condition thought to favor the evolution of
234 iteroparity and longer lifespan (Bulmer 1985, Orzack and Tuljapurkar 1989, Stearns 1992).
235 Thus, good environmental conditions should result in quicker attainment of the critical size
236 required for flowering (Lacey 1986). However, we suggest that large size may also be
237 detrimental under some conditions, for example if good environmental conditions lead to high
238 growth in the first year, that in turn may lead to higher levels of intraspecific competition.
239 Nonetheless, in this experiment, individuals were spaced at a distance to avoid such
240 competition, although natural *Plantago* individuals also occurred within field plots.

241 Strong maternal effects determining the number of reproductive years suggest the
242 importance of non-genetic means of inheritance in determining reproduction and reproductive
243 schedules. Maternal environment impacts many kinds of traits important to the fitness of
244 organisms, ranging from aspects of metabolism tied to cellular structures, to seed chemical
245 composition, to fruit characteristics (Roach and Wulff 1987, Mousseau and Fox 1998).
246 Although maternal effects dominate the early life of plants more than they do the later life
247 (Weiner et al. 1997), nonetheless maternal effects can be long-lasting, as they are in
248 determining the number of reproductive years experienced by plants (Roach and Wulff 1987).

249 Our work reinforces that in iteroparous perennial plants, greater numbers of reproductive

250 years typically lead to greater fitness (Lacey et al. 1983, Silvertown 1983, 1986). However,
251 long-lived herbaceous perennials have more variable fecundity than shorter-lived perennials
252 (García et al. 2008), most likely owing to a need to maintain fitness via high adult survival
253 (Sæther and Bakke 2000, Miller et al. 2008). Although *Plantago lanceolata* is an iteroparous
254 perennial, in our study 46.7% of reproducing individuals only reproduced once, and did so
255 overwhelmingly in the first or second years of life. Thus, the adaptive benefits do not mesh with
256 the commonality of single reproductive bouts. One possible reason may be that the reproductive
257 schedule of this plant is at least partially determined by spatial differences in microhabitat.
258 Under limited nutrients, some plants may not reach the proper threshold sizes necessary to
259 ensure multiple reproductive bouts (Wilbur and Collins 1973, Lacey 1986). Another possible
260 scenario is that plants reproducing only once may minimize the variance in fitness over
261 generations, leading to increased geometric mean fitness relative to plants reproducing more
262 often. Such a bet-hedging strategy may result in fewer reproductive episodes yielding higher
263 fitness under some conditions, and could be verified via a multiple cohort study conducted over
264 multiple generations. We suggest further work to clarify this apparent contradiction.

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373 TABLE 1. Logistic regression of the probability of flowering as a function of early-life size,
 374 lifespan, block, cohort, and paternal lineage in four cohorts of an experimental population of
 375 *Plantago lanceolata* in Shadwell, Virginia. Each cohort analyzed separately. The coefficient *b*
 376 refers to the logit-untransformed regression coefficient. Sire, cohort, and block are categorical
 377 variables and so no coefficient is given.

<i>Factor</i>	<i>b</i> ± 1 <i>SE</i>	<i>Wald coefficient</i>	<i>df</i>	<i>P</i>
Cohort		10.363	3	0.016
Block		34.599	16	0.005
Sire		22.793	19	0.247
Size	0.432 ± 0.096	20.143	1	<0.001
Lifespan	0.118 ± 0.019	40.019	1	<0.001
Cohort × Block		64.244	38	0.005
Cohort × Sire		87.814	57	0.005
Cohort × Size		54.358	3	<0.001
Cohort × Lifespan		25.705	3	<0.001
Block × Sire		292.253	304	0.676
Block × Size		66.633	16	<0.001

Block × Lifespan		48.222	16	<0.001
Sire × Size		39.196	19	0.004
Sire × Lifespan		63.385	19	<0.001
Size × Lifespan	-0.003 ± 0.001	26.356	1	<0.001

379 TABLE 2. Variance components determining the number of reproductive years in four cohorts of
 380 an experimental population of *Plantago lanceolata* in Shadwell, Virginia. Results are shown by
 381 cohort.

<i>Source</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>Prop. of var.</i>	<i>P</i>
Cohort 1					
Dam	77.348	10	7.735	0.008	0.021
Sire	35.620	15	2.375	<0.001	0.515
Sire × Dam	36.329	15	2.422	0.009	0.001
Error	6502.588	6614	0.983	0.983	
Cohort 2					
Dam	146.061	10	14.606	0.015	<0.0001
Sire	57.681	15	3.845	0.006	0.031
Sire × Dam	21.169	15	1.411	0.002	0.117
Error	7669.442	7852	0.977	0.977	
Cohort 3					

Dam	136.365	10	13.637	0.031	<0.001
Sire	52.045	15	3.470	0.012	0.047
Sire × Dam	15.598	12	1.300	0.004	0.176
Error	3397.252	3565	0.953	0.953	
Cohort 4					
Dam	22.591	4	5.648	0.012	0.048
Sire	21.258	20	1.063	-0.011 (0)	0.814
Sire × Dam	18.265	11	1.660	0.008	0.073
Error	3194.803	3223	0.991	0.991	

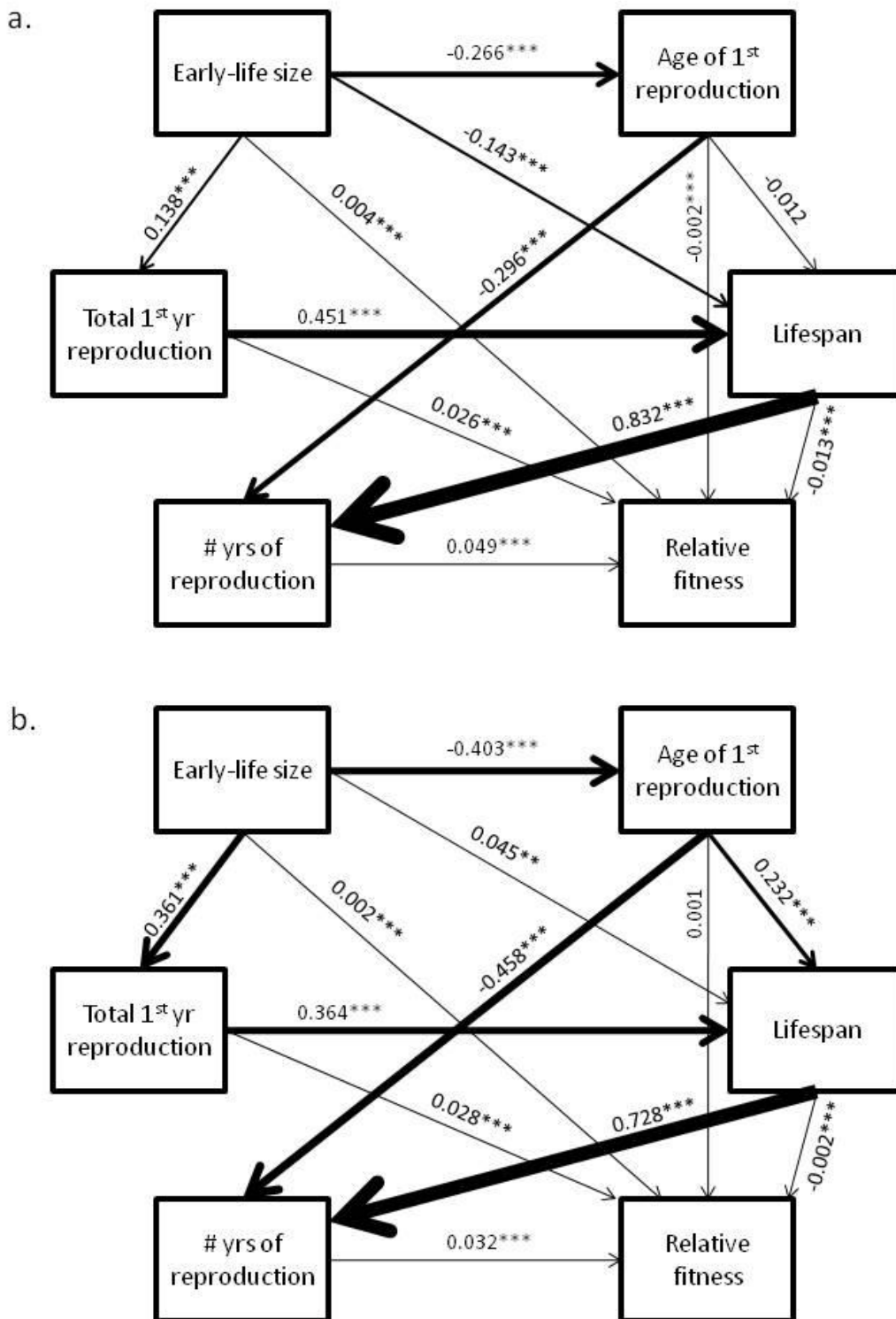
382 FIGURE LEGENDS

383 FIGURE 1. Path diagrams resulting from structural equation modeling of factors affecting
384 relative fitness in four cohorts of an experimental population of *Plantago lanceolata* in
385 Shadwell, Virginia. Results for cohorts 1, 2, 3, and 4 are shown in figures 1a, 1b, 1c, and 1d,
386 respectively. Factors tested include size attained in the first year of life (i.e., early-life size), age
387 of first reproduction, total first year reproduction, lifespan, and the number of reproductive
388 years. Here, early-life size is an exogenous variable, while all other variables are endogenous.
389 Arrow thickness indicates strength of causality. Asterisks indicate significance (No asterisk: $P >$
390 0.05 ; * $0.01 < P \leq 0.05$; ** $0.001 < P \leq 0.01$; *** $P \leq 0.001$).

391 FIGURE 2. Proportion of individuals flowering from one to six times by cohort in an
392 experimental population of *Plantago lanceolata* growing in Shadwell, Virginia. In this analysis,
393 each year of flowering is considered to be a single reproductive event.

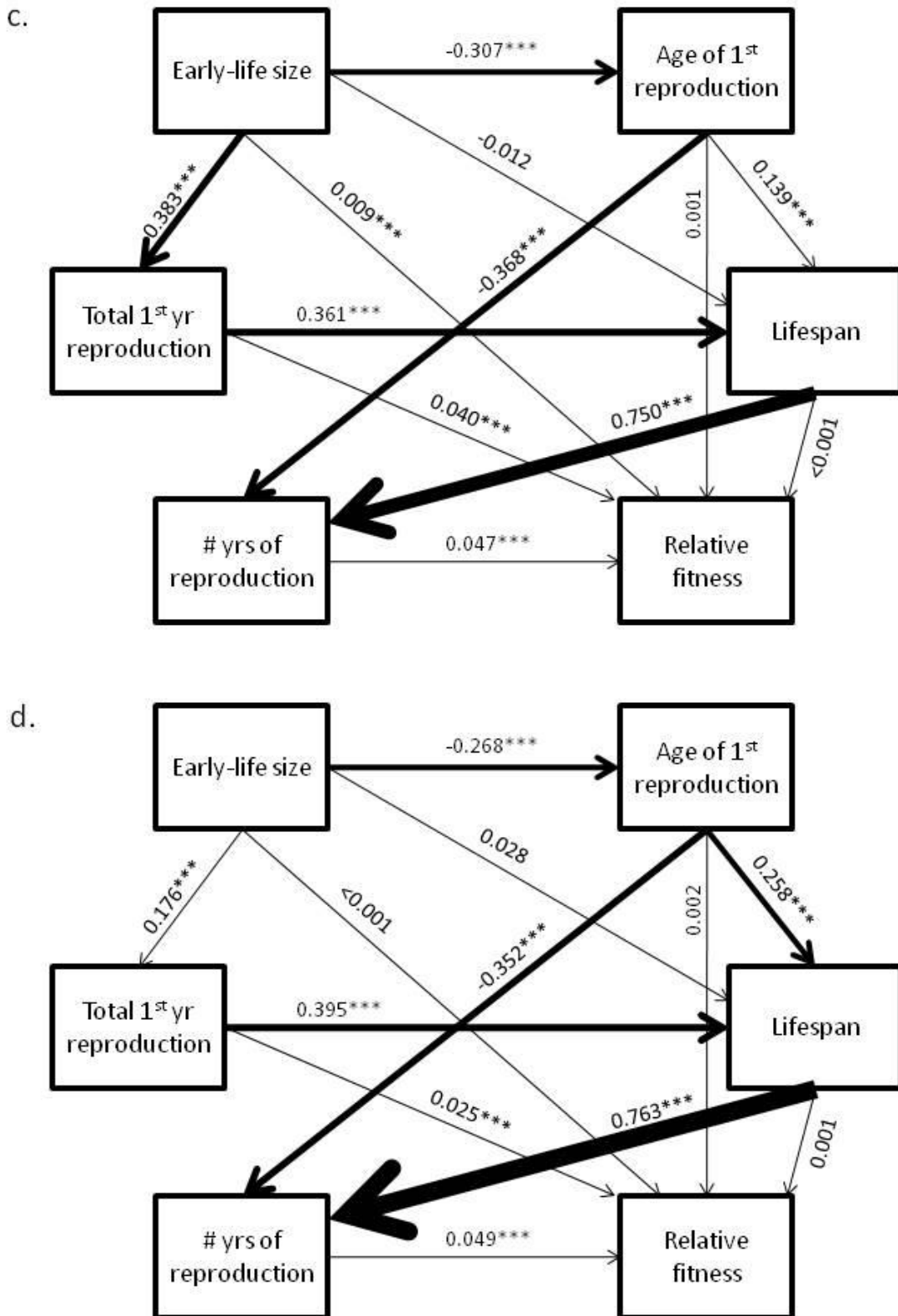
394 FIGURE 3. Proportion of plants reproducing only once in their lifetimes, per cohort flowering in
395 each year after planting in an experimental population of *Plantago lanceolata* in Shadwell,
396 Virginia.

397 FIGURE 1.

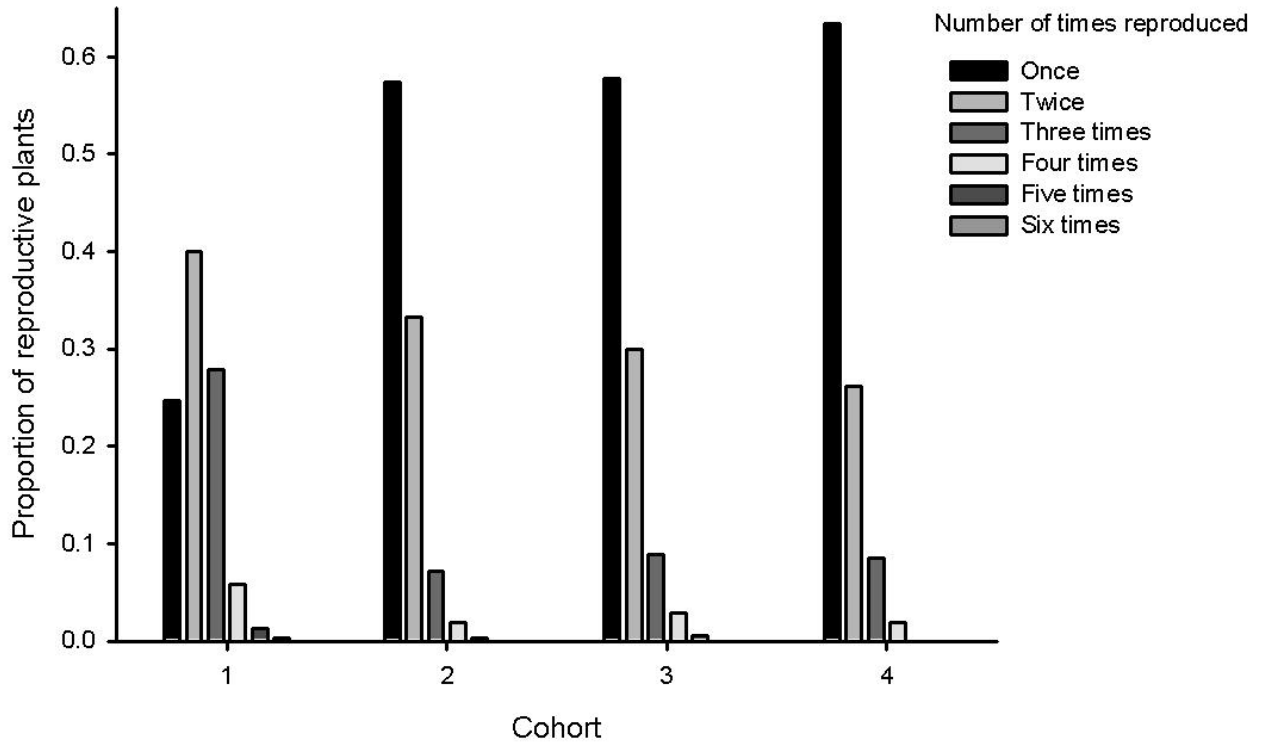


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401 Figure 1 (cont.).

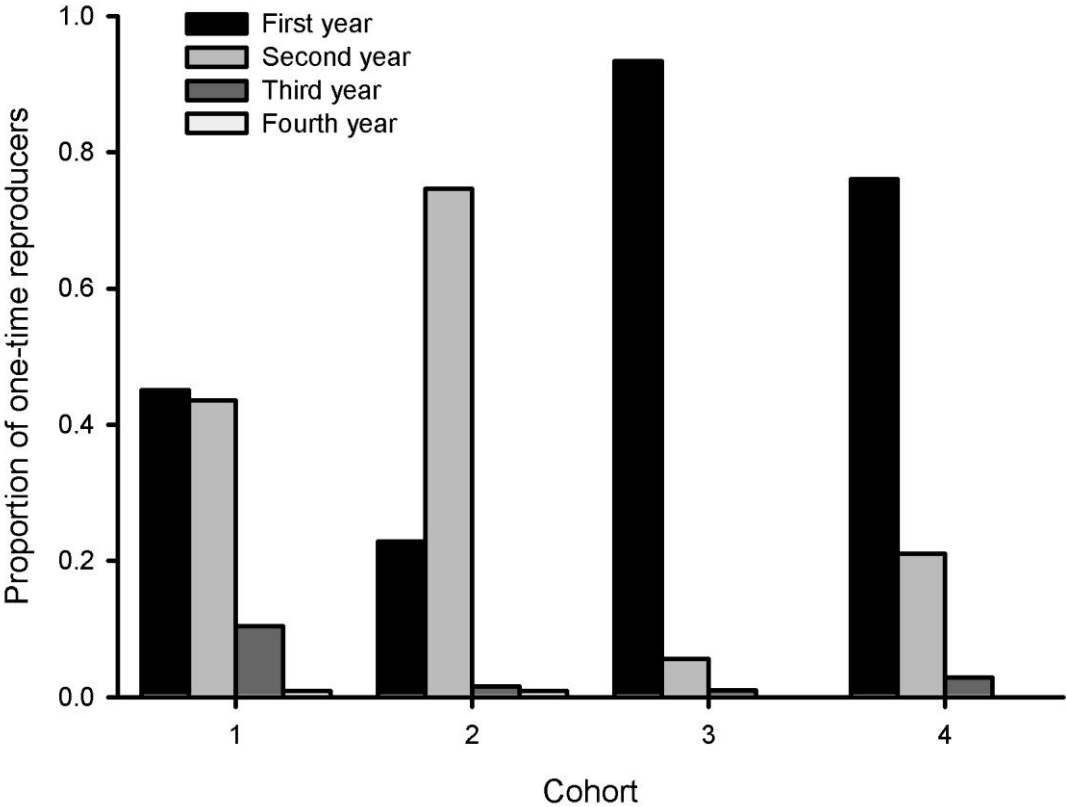


403 FIGURE 2.



404
405
406

407 FIGURE 3.



408

409 ELECTRONIC APPENDIX S1. Path coefficients from structural equation modeling of relative fitness as a function of size attained in the
 410 first year of life (i.e., early-life size), age of first reproduction, total first year reproduction, lifespan, and the number of reproductive
 411 years in four cohorts of an experimental population of *Plantago lanceolata* in Shadwell, Virginia. The structural equation model is
 412 presented in Figure 1. Asterisks indicate significance (No asterisk: $P > 0.05$; * $0.01 < P \leq 0.05$; ** $0.001 < P \leq 0.01$; *** $P \leq 0.001$).

		<i>Cohort 1</i>	<i>Cohort 2</i>	<i>Cohort 3</i>	<i>Cohort 4</i>
<i>From</i>	<i>To</i>	<i>Est ± SE</i>	<i>Est ± SE</i>	<i>Est ± SE</i>	<i>Est ± SE</i>
Early-life size	Age 1 st repr	-0.266 ± 0.016***	-0.403 ± 0.013***	-0.307 ± 0.029***	-0.268 ± 0.035***
Early-life size	Total 1 st yr repr	0.138 ± 0.016***	0.361 ± 0.012***	0.383 ± 0.025***	0.176 ± 0.029***
Early-life size	Lifespan	-0.143 ± 0.015***	0.045 ± 0.014**	-0.012 ± 0.032	0.028 ± 0.031
Age 1 st repr	Lifespan	-0.012 ± 0.015	0.232 ± 0.014***	0.139 ± 0.021***	0.258 ± 0.023***
Total 1 st yr repr	Lifespan	0.451 ± 0.011***	0.364 ± 0.011***	0.361 ± 0.019***	0.395 ± 0.017***
Age 1 st repr	# reprod yrs	-0.296 ± 0.008***	-0.458 ± 0.008***	-0.368 ± 0.012***	-0.352 ± 0.015***

Iteroparity in *Plantago*

Shefferson and Roach

Lifespan	# reprod yrs	$0.832 \pm 0.007^{***}$	$0.728 \pm 0.008^{***}$	$0.750 \pm 0.011^{***}$	$0.763 \pm 0.013^{***}$
Early-life size	Rel. fitness	$0.004 \pm 0.001^{***}$	$0.002 \pm 0.000^{***}$	$0.009 \pm 0.002^{***}$	0.000 ± 0.002
Age 1 st repr	Rel. fitness	$-0.002 \pm 0.001^{***}$	0.001 ± 0.001	0.001 ± 0.001	0.002 ± 0.001
Total 1 st yr repr	Rel. fitness	$0.026 \pm 0.001^{***}$	$0.028 \pm 0.000^{***}$	$0.040 \pm 0.001^{***}$	$0.025 \pm 0.001^{***}$
Lifespan	Rel. fitness	$-0.013 \pm 0.001^{***}$	$-0.002 \pm 0.001^{***}$	0.000 ± 0.001	0.001 ± 0.001
# reprod yrs	Rel. fitness	$0.049 \pm 0.001^{***}$	$0.032 \pm 0.001^{***}$	$0.047 \pm 0.002^{***}$	$0.049 \pm 0.001^{***}$